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# THE HOMING OF THE MUD-DAUBER.

C. H. TURNER.

## INTRODUCTION.

In my paper on "The Homing of Ants"<sup>1</sup> there is recorded evidence that ants find the way home neither by a homing instinct nor by reflex action nor merely by kinesthetic responses; but by utilizing landmarks. In this paper I propose to record experimental evidence that the same is true of the common mud-dauber wasps.

It has long been recorded by keen observers that both the social and the solitary wasps, on leaving their nests for the first time, carefully examine the surroundings before flying away. It is also stated by some that any alteration in the immediate surroundings of the nest will render it difficult, or even impossible, for the wasp to find its way back again.

Mr. and Mrs. Peckham, who have devoted much time to the study of both the social and the solitary wasps, say: <sup>2</sup> "If they were furnished with an innate sense of direction they would not need to make a study of the locality of the nest in order to find the way back, but if they were without this sense it would be only common prudence to take a good account of their bearings before going far afield. . . . In reading much of the popular natural history of the day one might suppose that the insects seen flying about on a summer's day were a part of some great throng which is ever moving onward, those that are here today being replaced by a new set tomorrow. Except during certain seasons the exact opposite is true. The flying things about us abide in the same locality and are the inhabitants of a fairly restricted area. The garden in which we worked was, to a large extent, the home of a limited number of certain species of wasps that had resided there from birth or, having found the place accidentally, had settled

<sup>1</sup> *Jour. of Comp. Neur. and Psy.*, Vol. XVII., pp. 367-434, Pl. II.-IV.

<sup>2</sup> G. W. and E. G. Peckham, "On the Instincts and Habits of the Solitary Wasps," Madison, Wis., 1898, pp. 212, 213, 215.

there permanently. . . . After days passed in flying about the garden — going up Bean Street and down Onion Avenue, time and again — one would think that any formal study of the precise locality of a nest might be omitted, but it was not so with our wasps. They made repeated and detailed studies of the surroundings of their nests. Moreover, when their prey was laid down for a moment on the way home, they felt the necessity of noting the place carefully before leaving it. . . . If the examination of the objects about the nest makes no impression upon the wasp, or if it is not remembered, she ought not to be inconvenienced nor thrown off her track when weeds and stones are removed and the surface of the ground is smoothed over; but this is just what happens. *Aporus fasciatus* entirely lost her way when we broke off the leaf that covered her nest, but found it, without trouble, when the missing object was replaced. All the species of *Cerceris* were extremely annoyed if we placed any new object near their nesting-places. Our *Ammophila* refused to make use of her burrow after we had drawn some deep lines in the dust before it. The same annoyance is exhibited when there is any change made near the spot upon which the prey of the wasp, whatever it may be, is placed. We learned from experience how important it was not to disarrange the grass or plants on such occasions."

All this was written before Bethe<sup>1</sup> had restated, with emphasis, his theory that bees (the morphological and physiological kinship of which to wasps leads one to expect them to be psychologically similar) are guided home by an unknown force; and before Pieron<sup>2</sup> had asserted that ants are led home by a reflex kinaesthetic sense. This being the state of affairs a crucial experiment seemed to be needed. The mud-dauber (*Sceliphron*, Klug = *Pelopæus*, Latr.) was selected, partly because its habits rendered it comparatively easy to obtain material and partly because, so far as I know, no such experiments have been performed upon it.

<sup>1</sup> A. Bethe, "Die Heimkehrfähigkeit der Ameisen u. Bienen zum Theil nach neuen Versuchen," *Biol. Centrbl.*, 2 Bd. (1902), no. 7, pp. 193-215; no. 8, pp. 234-238.

<sup>2</sup> H. Pieron, "Du rôle sense musculaire dans l'orientation des fourmis," *Bull. Inst. Gen. Psy. Paris*, T. 4 (1904), pp. 168-187.

## PRELIMINARY OBSERVATIONS.

These preliminary observations were made in a laboratory the walls of which were ceiled with tongue-and-grooved pine boards. These boards were arranged vertically. Two of the walls were supplied with windows and two were not. Near the top of each of these walls mud-daubers constructed nests. Some of these nests were in dark places and some were in light places. I noticed that the wasp never flew directly to the nest, but that it would alight on a certain crack. After ascending, afoot, this crack, until it had reached the height of the nest, it would turn and walk to it. The same wasp always alighted on the same crack and at about the same distance from the floor. This led me to suppose that wasps used the cracks as landmarks. In this room a certain window was lowered from the top, through which opening the wasps came and departed. In another room, in which similar experiments were conducted, the window was raised from the bottom. Wasps frequented this room as much as they did the other. Evidently wasps can learn the way into a room by either a high or a low opening.

## THE ENVIRONMENT OF THE EXPERIMENTS.

This series of experiments was performed in a laboratory thirty-seven and a half feet long, twenty-five feet wide and twelve feet

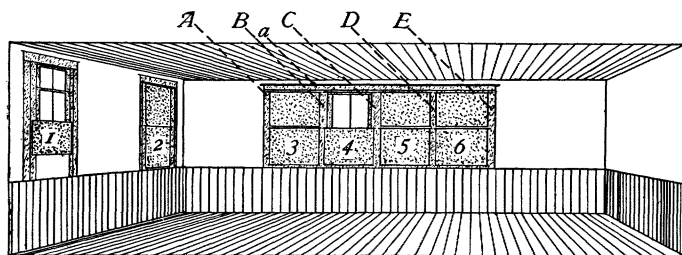


FIG. 1. This is a diagram of the room arranged for experiment one. 1-6, windows; A-E, upright facings of windows; a, location of the nest. The wood-work of the windows is shaded with broken lines, the window-shades with dots. The boards in the floor, ceiling and dado are drawn twice as wide as they were.

high (Fig. 1) which was situated in the third story of a large brick building. The ceiling was covered with tongue-and-grooved pine boards and a four-foot dado of pine ceiling extended around

the lower third of the walls of the room. Excepting the space occupied by windows, doors and dado, the walls were plastered in the rough. In the west wall there were two windows (Fig. 1, 1 and 2); in the north, four (Fig. 1, 3 to 6). The windows of the north wall were close together, being separated by wooden partitions only one foot wide (Fig. 1, *B, C, D*). Across the top of each window there was a piece of three inch moulding. On the north wall this moulding extended continuously across the four windows. There were two green blinds to each window, one to each sash. These blinds were not quite opaque. The ceiling was painted green; the walls, including dado, doors and window-facings, cream color.

In order to have only one entrance for the wasps, the lower sash of window number one was raised half way. All other windows were closed. This condition was maintained throughout the entire series of experiments. To furnish definite light relations for the beginning of the experiment, the lower shade of window number one was raised about half way and the top shades of windows one and three raised as far as possible. All the other shades were down. After these conditions had been maintained for nearly two weeks a mud-dauber began the construction of a nest on the moulding above window number three at a point about six inches from upright *B* (Fig. 1, *a*).

When first discovered the wasp had completed nearly half of one cell; hence it had already made several trips back and forth through window number one. I watched the wasp make several trips, and each time it behaved as follows. On entering the room it would fly obliquely upwards to the upper third of upright *B*. Then it would fly vertically upwards almost to the ceiling, thence it would fly leftward to the nest. The line of flight from the entrance to upright *B* was perceptibly curved, the convexity being towards the east. The flight from the entrance through window number one to the nest consumed about half a minute. In departing, the wasp flew downwards in a curve from the nest to the upper portion of the opening through which it had entered the room. After watching the wasp make several trips in practically the same manner, the following experiments were performed:

## EXPERIMENT 1.

*The lower shade of window number one was raised half way and the top shade as far as it would go. While the wasp was out of the room, all the blinds of windows number two to six were closed except the upper shade of window number four, which was raised as far as possible (Fig. 1).*

The wasp on entering through window number one flew obliquely upwards across the beam of light from window number four to the upper third of upright *C*. (This line of flight was convex towards the east.) It then flew vertically upwards almost to the ceiling then leftward about a foot (this is a little more than the distance of the nest from upright *B*) and examined carefully the moulding. Not finding the nest, it began flying first to the right and then to the left in constantly elongating ellipses with very short minor axes. All this time it was carefully examining the moulding. Occasionally the mud-dauber would fly downward into the beam of light and then resume its search. In its lateral flights the wasp sometimes flew as far to the east as upright *D* and to the west almost as far as upright *B*. At the end of three minutes it had not found the nest, although under former conditions of illumination it required only half a minute to fly from window number one to the nest.

*While the wasp was still searching for the nest, the top shade of window number four was lowered and the corresponding shade of window number three raised as far as possible. This reproduced the conditions under which the wasp had originally worked.*

Almost immediately the wasp found the nest!

## EXPERIMENT 2.

*The lower shade of window number one was raised half way and the top shade as far as possible. While the wasp was out of doors, all the shades of windows number two to six were lowered except the top shade of window number five, which was raised as high as possible.*

On entering, the wasp flew in a fairly direct line towards the nest. When about one third of the way across the room, it returned almost to window number one and described a circle of about a foot in diameter. It then flew to the middle of the upper

shade of window number four. Thence it flew upwards almost to the ceiling and then leftward to the nest.

#### EXPERIMENT 3.

*The lower shade of window number one was raised half way and the upper shade as far as possible. All of the shades of windows number two to six were lowered except the top shade of window number three, which was raised as far as possible. This reproduced the conditions under which the wasp had worked originally.*

On entering the room the wasp flew obliquely upwards to the upper third of upright *B*. Then it flew vertically upwards almost to the ceiling. Thence it flew leftward to the nest. The line of flight from the entrance to upright *B* was perceptibly curved, the convexity extending towards the east. The total flight from the entrance to the nest consumed about half a minute. The shades were maintained in the above position until the mud-dauber had made three trips. Each was made in practically the same manner.

#### EXPERIMENT 4.

*The same conditions as in experiment one.*

The behavior was practically the same as in experiment one. In this experiment, however, the shades were maintained in the same position until the wasp had found the nest, which required nearly five minutes.

The wasp was allowed to make two trips. Its behavior on the second trip resembled that on the first ; but it required only three minutes to pass from the entrance to the nest.

#### EXPERIMENT 5.

*The same conditions as in experiment three.*

The wasp behaved the same as in experiment three.

#### EXPERIMENT 6.

*The lower shade of window number one was raised half way and the top shade as high as possible. All of the shades of windows two to six were lowered, except the top shade of window number two, which was raised as far as possible.*

The wasp on entering the room described a small circle then

flew obliquely upwards to a point almost to the ceiling, but a little to the west of upright *A*. It then flew alternately leftward and rightward until the nest was found, which consumed about one minute.

The wasp was allowed to make two trips. Its behavior on the second trip was similar to that on the first, and about the same amount of time was consumed in passing from the entrance to the nest.

#### EXPERIMENT 7.

*The conditions were the same as in experiments three and five.*

The wasp was permitted to make two trips. It behaved the same as it did in experiments three and five.

#### EXPERIMENT 8.

*The lower shade of window number one was raised half way and the top shade as high as possible. All the shades of windows two to four were lowered.*

On entering the room the wasp described several small circles. It then flew first to about the middle of the upper sash of window number three, then to window number two, then to window number five. Finally, after much searching, the nest was found.

The shades were retained in the above condition until the wasp had made two trips. On the second trip it went first to upright *C* and then, after a short search, it found the nest.

#### EXPERIMENT 9.

*The same conditions as in experiments three, five and seven.*

The behavior was the same as in experiments three, five and seven. Two trips were made.

#### EXPERIMENT 10.

*At first the conditions were the same as in experiment eight. While the wasp was on the nest, the top shade of window number one was lowered.*

On leaving the nest the wasp flew away through the window in its usual way. The lowering of the top shade of window *A* did not change its behavior.



## EXPERIMENT 11.

*The lower shade of window number one was raised half way and the top shade lowered. While the wasp was out of doors, all the shades of windows two to six were lowered except the top shade of window three, which was raised as high as possible.*

The wasp behaved the same as in experiments three, five, seven and nine.

## EXPERIMENT 12.

*The lower shade of window number one was raised half way. While the wasp was out of doors, all of the other shades were lowered.*

The wasp behaved the same as in experiment eight.

## EXPERIMENT 13.

*The lower shade of window number one was raised about half way. While the wasp was out of doors, all the shades of windows two to six were lowered except the lower shade of window number three, which was raised as far as possible.*

At first the wasp searched carefully the upper portion of the wall to the west of the upright *A*. Then, as a result of extending its search to the east, the nest was discovered.

This experiment was repeated with the same results.

## EXPERIMENT 14.

*The same conditions as in experiments three, five, seven, nine and eleven.*

The wasp behaved the same as it did in experiments three, five, seven, nine and eleven.

## EXPERIMENT 15.

*The same conditions as in experiment one.*

The wasp behaved as in experiment one. It took about one minute to find the nest. The wasp was allowed to make two trips.

## EXPERIMENT 16.

*The same conditions as in experiment one.*

After the shades had been maintained in this position for about two days, the wasp on entering the room flew obliquely upwards

to near the top of upright *C* and then obliquely leftward and upwards to the nest. The trip from window number one to the nest consumed much less than a minute.

#### EXPERIMENT 17.<sup>1</sup>

*The same conditions as in experiment three. This experiment was performed immediately after the close of experiment sixteen.*

The wasp on entering the room flew obliquely upwards, across window number four, to the upper third of upright *C*; then obliquely leftward and upwards, across windows number four and three, to a little beyond the upright *A*. It then searched about until the nest was found.

*The shades were left in this condition from 10:45 A. M. July 19 to 9 A. M. July 20, at which time the wasp occasionally visited the nest. The wasp on entering the room, flew obliquely upwards, across window number three, to the upper third of upright *B*; then leftward, across window number three, to a little beyond upright *A*, then obliquely rightward and upwards to the nest. The conditions in this experiment and in experiments three, five, seven, nine and eleven are identical, yet the behavior in this case is quite unlike what it was in those. Evidently prolonged exposure to the conditions described in experiment sixteen has modified the behavior of the wasp. It had lost (forgotten) its old response to the conditions described in experiment three and been forced to acquire a new response.*

#### CONCLUSIONS.

From these experiments it is evident that, in finding its way back to its nest, the mud-dauber is guided neither by what is known as a homing instinct nor by what Pieron has called a kinesthetic reflex; for if either assumption were true, a manipulation of the light should not have altered the wasp's behavior.

Evidently light plays a prominent rôle in the homing of wasps, yet the behavior of the mud-dauber is not a phototropism; for in

<sup>1</sup> This series of experiments was begun on the morning of July 17, 1908, and ended on the morning of July 20, 1908. Experiments one to fifteen inclusive were performed the first day and in the order mentioned. The intervals between the experiments were only sufficiently long to permit the necessary adjustments to be made. Between experiments fifteen and sixteen there was an intermission of almost two days; between experiments sixteen and seventeen, an intermission of five minutes.

no case did the wasp so orient itself as to have the major axis of its body parallel to the rays of light. Furthermore in hunting for the nest, the wasp crossed the light sometimes in one direction and sometimes in another. In yet other cases the wasp would zigzag across the light.

Neither is the wasp's behavior merely a reflex response either to brightness or to the direction of the rays of light; for if that were the case, in experiment six, when all the shades of windows number two to four were lowered except the top shade of window number two, the wasp should have flown, not to the wall to the west of window number three, but to window number two. Likewise in experiment eight, when all the shades of windows number two to six were lowered and the only bright light entering the room was that which came through the upper and lower portions of window number one, if the wasp were guided merely by light acting reflexly, then it should not have been able to find the nest at all. Furthermore, if the wasp's behavior is merely a reflex response to light, there is no reason why it should have entered the room at all, for the open portion of the window was certainly not so bright as the window-panes from which the light was reflected. We say nothing about the bright sunshine out of doors!

But brightness is not the only factor which influences the movements of this wasp; else, when all the shades of windows number two to six were lowered, it would have been impossible for it to rediscover the nest. This series of experiments warrants the induction that, in the wasp's memory, that nest is located in a certain direction and at about a definite distance from a bright patch which is situated at a known elevation in a peculiar environment.

The above statement predicates to wasps memory and an awareness of space relations. As to the existence of memory these experiments furnish unequivocal evidence. This harmonizes with the views of Forel and the Peckhams. In "The Homing of Ants" are recorded proofs that ants have an awareness of space relations, and, since wasps are near kin to ants, it is probable that they, too, have an awareness of space relations. This series of experiments furnishes evidence to support this view. In

almost every experiment of this series the lower shade of window number one was raised half way and the top curtain all of the way. This was done in order to have the departing wasp confronted, on each trip, by an upper and a lower bright patch. Were the wasp responding to a bright patch merely and not to a bright patch in a definite place, then the wasp should have flown to the upper bright patch just about as often as it did to the lower. The wasp always flew directly from the nest to the opening in window number one! There was but one exception to this statement. On one occasion I was standing on a ladder watching the wasp construct the nest. I was within two feet of the nest. On that occasion the wasp, on departing, circled about once or twice and then returned to the nest and from there flew to the exit.

In brief, these experiments warrant the conclusion that the flying mud-dauber, like the creeping ant, is guided by certain landmarks, and that light plays a prominent rôle in furnishing such landmarks.

HAINES NORMAL SCHOOL,  
AUGUSTA, GA., July 25, 1908.